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THE STRUCTURE OF CILIA, ESPECIALLY IN GASTROPODS

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We venture to present the following incomplete observations in the hope that they may contribute to the solution of the difficult problem of the structure of cilia.

While looking over fresh marine plankton from Narragansett Bay, we came upon an unidentified but common larva of a protobranch mollusk whose velar cilia were so large that they were exceptionally favorable for study. With a cover glass upon the larva, we were able to watch with increasing ease the successive ciliary waves which gradually became less frequent and rapid as the animal died; and consequently we were able to study the individual cilia in detail. A groove with overhanging edges follows the rim of the velum, and the large preoral cilia are arranged in a row along the posterior edge of this groove. Each cilium is large and somewhat curved, being concave on the side toward which the effective stroke is directed. It tapers evenly from its basal body to its apex. The protoplasm at the base of the cilium was seen to contract alternately on the opposite sides of the basal body and, correspondingly, to move the base of the cilium back and forth. In contracting, the protoplasm draws the cuticula downward.

As already stated, the cilia are arranged in a row along the edge of a groove. The contraction of the protoplasm upon the lower side of the cilium draws its base into the groove while the lower portion of the cilium is bent so as to fit into the groove and the upper portion is carried backward a few degrees (Fig. 1, *a* and *b*). The convex side of the cilium is thus drawn into the groove. The

contraction of the protoplasm above the cilium carries its base upward, and cramps the cilium against the overhanging edge of the groove until the lower portion of the cilium is bent into an S-shaped curve (Fig. 1, *c* and *d*). The contraction continuing, the cilium is forced past the edge of the groove and flies out and back with a very rapid stroke — the effective stroke of the cilium (Fig. 1, *e*). It is carried by the force of its stroke far beyond its position of rest to which its elasticity brings it back in position for another stroke. There seems no doubt that these cilia are elastic rods (Fig. 2, *g*) which are moved by the contraction of the protoplasm at their bases. The cuticula around the base of the cilium rises and falls with the movement of the cilium as though it formed a plate into which the cilium is set. Consequently it appears that the contractile fibrillae of the protoplasm are inserted in the cuticula and not directly in the base of the cilium. We do not know what part the basal body plays in this movement but we believe that it forms a pivot upon which the cilium turns somewhat as an echinoderm spine turns upon its base.

The cramping and subsequent escape of the cilium account for the rapidity and force of the effective stroke and also explain the well known fact that the cilia of rotifers and veligers always seem to move only in the opposite direction to that which is necessary, since the effective stroke is too rapid to be visible. We do not believe that the groove is a common ciliary structure,— on the contrary it is probably present only in cilia like those mentioned, whose effective stroke is invisible. However, we should call attention to the pits, collars, and ridges at the bases of the flagella and cilia of Protozoa, Porifera, and spermatozoa to which as yet no function has been ascribed.

Almost every cilium whose structure has been made out consists of an axial rod or canal filled with cell sap or protoplasm, and a sheath consisting of cuticle or protoplasm. In the velar cilium described above, we have no doubt that the elastic rod is surrounded by a protoplasmic or cuticular sheath.

The large swimming plates of ctenophores, which are formed by the fusion of a number of cilia, have been carefully studied by Verworn.[1] In the position of rest, the plate is parallel to the sur-

[1] Verworn, M. Studien zur Physiologie der Flimmerbewegung. *Arch. f. d. g. Physiol.*, 1891, 48, p. 149–180.

face of the body and points toward the aboral pole of the animal. Its base is sharply bent toward the aboral pole and its distal portion is concave outward. The contraction of the oral side of the base of the plate first straightens out the basal curve and then bends the base of the cilium over toward the mouth. While the contraction of the base is taking place the distal portion of the plate is first flattened by the resistance of the water and then is bent into a curve of shorter radius by the contraction of its oral side. At the end of the stroke, the cilium is again parallel to the surface

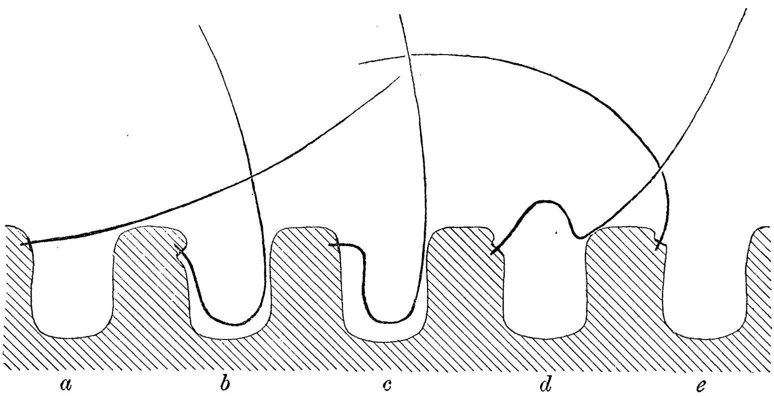

FIG. 1.— Diagram showing successive stages in the stroke of a cilium in the velum of a gastropod larva.

of the animal but it points toward the mouth and its single concavity is directed inward. Smooth muscle fibers pass from the gastric canal, which underlies each row of cilia, to the rib which carries the swimming plates; by their contraction they draw the rib into the gelatinous tissue of the body. Verworn believes that the sole function of these muscle cells is to draw the plates from the surface for the protection of the plates, and also that the movement of the cilium is caused chiefly by the contraction of its base. He does not suggest the existence of an axial supporting rod. It is possible, however, that the muscles underlying the plates may assist in the movements of the cilium and that it is really quite similar functionally to the velar cilia.

The tails or flagella of spermatozoa undoubtedly consist of an

axial rod with a protoplasmic sheath which often bears undulatory membranes. The tails of the vast majority of spermatozoa seem to lack the power of movement when separated from the basal body and cell protoplasm, and we believe that this indicates a dependence of the cilium upon a muscle-like structure around the basal body. In Salamandra, as reported by Meves,[1] and in many protozoa a

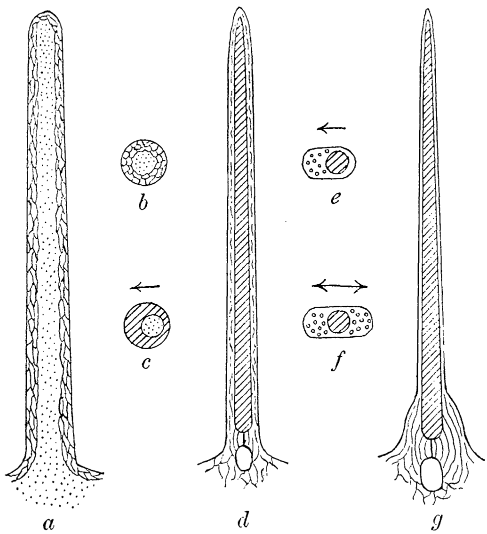

Fig. 2.— Diagram showing the hypothetical structure cilia.
a, primitive cilium with fluid core and contractile sheath.
b, cross section of *a*.
c cross section of a cilium according to Schäfer's theory of ciliary structure.
d, more highly developed cilium with basal body and elastic axial rod.
e, cross section of an irreversible cilium.
f, cross section of a reversible cilium.
g, cilium in which the contractile portion is confined to its base.

flagellum or cilium separated from the basal body and the cell protoplasm is capable of motion. In these cases doubtless the contractile substance is not confined to the base of the flagellum but extends into, perhaps throughout, the sheath (Fig. 2, *d*). The vast majority of cilia and flagella, however, can move only while in connection with protoplasm and the basal body. A different interpretation has been given to these facts by Pütter[2] and

[1] Meves, F. Über Structur und Histogenese der Samenfäden des Meerschweinchen. *Arch. f. mikr. Anat.*, 1899, 54, p. 329–402, vide p. 382.

[2] Pütter, A. Die Flimmerbewegung. *Erg. Physiol.*, 1902, 2, Abth. 2, p. 1–102.

others who consider that the isolated cilium is capable of motion but lacks only the necessary stimulus.

That the core or axis of the cilium is always solid is rendered improbable by the fact that many pseudopodia and the tentacles of the Suctoria, which are admittedly homologous with cilia, clearly have a central canal or a fluid core (Fig. 2, *a*). Moreover the experiments of Zacharias [1] who caused the spermatozoa of Polyphemus to produce slender cilia-like pseudopodia by immersing them in a 5 per cent. solution of sodium phosphate, and of Prowazek [2] who saw the retracting protoplasm of an injured cell thread of *Siphonaea bryopsis* produce in five minutes cilia which beat at the rate of 40 strokes a minute, and who [3] also found in Chilomonas cilia appearing as small processes which in 8 minutes attained half their normal size and beat 19 times in 20 seconds, show that certain cilia must consist of but slightly modified protoplasm. These experiments also indicate that a solid or a permanent core is not always formed, for in the first two cases the cilia were quickly destroyed. It is clear that a tube containing a fluid which cannot escape either because of the cell turgor or because enclosed in the tube, will act precisely as an elastic solid. In this connection Gurwitsch's[4] discovery that a marked increase in cell turgor accompanies the formation of cilia, and the cases of contraction of the cell or movements of the nucleus indicating such contraction, synchronously with the stroke of the cilia of the cell, all suggest that the turgor holds in, or the contraction of the cell forces into, the cilium the fluid which forms its support. This consideration in turn suggests a function for the ciliary roots which may increase the turgor of the cell by drawing its walls together.

These various considerations have been utilized in the current theories of ciliary action and structure, especially in the most generally accepted theory which is supported with various modi-

[1] Zacharias, O. Über die Amöboiden Bewegungen der Spermatozoen von Polyphemus pediculus. *Zeit. f. wiss. Zool.*, 1885, 41, p. 252–258.

[2] Prowazek. Protozoenstudien II. *Arb. a. d. Zool. Inst. Univ. Wien*, 1900, 12, p. 243–300.

[3] Prowazek. Protistenstudien III. *Arb. a. d. Zool. Inst. Univ. Wien*, 1902, 14, p. 81–88.

[4] Gurwitsch, A. Studien uber Flimmerzellen. I. Histogenese der Flimmerzeller. *Arch. f. mikr. Anat.*, 1901, 57, p. 184–229.

fications by Engelmann,[1] Pütter, Parker[2] and Gurwitsch.[3] According to this theory, the cilium consists of an axial support and a contractile protoplasmic sheath. The nature of the axis has been less the subject of discussion than that of the sheath which Engelmann regards as fibrillar, Pütter as protoplasm with temporary fibrillar arrangements, and Gurwitsch as protoplasm of changing surface tension. As stated above, Verworn thinks that the cilium of ctenophores is formed of two columns of contractile protoplasm whose differential contraction moves the cilium, and Engelmann seems to lean toward this view.

Less generally accepted theories are those of Benda and Schäfer. Benda[4] believes that the cilium is passive and is operated by a mechanism at its base, but the cases cited above of the movement of cilia entirely separated from the basal body and the cytoplasm, and the failure with few exceptions to find such a mechanism, make this view unacceptable. The velar cilia above described, the existence in some cells of the hypobasal layer which seems to consist of contractile protoplasm, and the partial agreement of Verworn's observations upon ctenophore cilia suggest, however, that although this theory will not apply to all cilia, it is the only theory which explains the action and structure of certain cilia.

Schäfer[5] regards the cilium as an elastic tube (Fig. 2, *c*), one side of which is less elastic than the rest, into which fluid flows or is forced causing the cilium to bend over toward its less elastic side.

This theory is plausible and the structure is mechanically possible but it fails to explain some points, as, for example, the reversal of ciliary action and the presence of axial rods in spermatozoan flagella. It seems, however, that the action of the suctorian tentacles which are evaginated and invaginated like the finger of a glove can only be explained by this theory.

[1] Engelmann, T. W. Cils Vibratils, in Richet's *Dictionaire de Physiologie*, Tome 3, 1898, p. 785–799. See also older works by the same author.

[2] Parker, G. H. The Reversal of Ciliary Movement in Metazoans. *Am. Journ. Physiol.*, 1905, 13, p. 1–16.

[3] Gurwitsch, A. Morphologie und Biologie der Zelle. Jena, 1904, vide p. 76 ff.

[4] Benda, C. Über neuer Darstellungsmethoden der Centralkörperchen. 1901, *Arch. f. Anat. und Physiol., Physiol. abth.*, 1901, p. 147–157.

[5] Schäfer, E. A. Theories of ciliary movement. *Anat. Anz.*, 1904, 24, p. 497–511. See also *Anat. Anz.*, 1905, 26, 517–521, and *Proc. Royal Soc. London,* 1891, 41, 193–198.

The generally accepted theory is undoubtedly correct but it can now be stated more fully than heretofore and can be, in a measure, harmonized with the less acceptable theories. All protoplasmic processes, cilia, flagella, pseudopodia, and suctorian tentacles, are of essentially the same structure and consist of a contractile protoplasmic sheath which encloses a solid or fluid supporting core. Primitively the sheath (Fig. 2, *a*) is contractile throughout and is not marked off structurally or functionally from the remainder of the ectoplasm. Secondarily the sheath becomes differentiated into contractile and noncontractile portions, the relations of which are shown in the following examples. The contractile protoplasm (Fig. 2, *g*) of velar cilia and ctenophore plates is practically confined to the base of the cilium. Parker has shown that in reversible cilia (Fig. 2, *f*) the contractile substance must occur in two opposite bands which in Metridium are on the oral and aboral sides of the supporting axis. Ordinarily the aboral band contracts more strongly than the other and drives water away from the mouth but certain organic and inorganic substances cause the oral band to contract more strongly and so to reverse the direction of the effective stroke and of the currents caused by it. Parker shows also that irreversible cilia (Fig. 2, *e*) probably have but one band of contractile material. Ballowitz[1] has shown that spermatozoan flagella have a fibrillar axial structure surrounded by a sheath of uneven thickness and Pütter with others have shown that the axial rod supports the irregular contractile protoplasmic sheath.

The core of the pseudopodium, which is to be regarded as the simplest cilium, is fluid. In higher stages of ciliary development a solid, which is elastic in cilia and flagella and inelastic in pendulous pseudopodia, replaces the fluid core.

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[1] Ballowitz, B. Untersuchungen über die Structur der Spermatozoen, zugleich ein Beitrag zur Lehre vom feineren Bau der kontractilen Elemente. *Arch. f. mikr. Anat.*, 1888, 32, p. 401–473.